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# NEST SITE SELECTION BY FLORIDA SCRUB-JAYS IN NATURAL AND HUMAN-MODIFIED HABITATS

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ABSTRACT.—Bird species having specialized nesting substrates could suffer reduced reproductive success in habitats modified by human activities where optimal nest sites may be in short supply. We examined nest sites of Florida Scrub-Jays (*Aphelocoma coerulescens*) in intact, natural oak scrub and in scrub islands embedded in a suburban matrix. Despite differences in vegetation structure between natural and suburban scrubs, scrub-jays used scrub oaks (*Quercus* spp.) as substrate for >80% of all nests in both habitats. Because of fire suppression, vegetation in suburban scrubs tended to be taller than in natural scrubs; however, in both habitats jays appeared to prefer shrubs slightly taller than those available. In both habitats, nest height increased with nest shrub height, but the relationship was stronger in suburbs. In suburbs, the height of nests relative to nest shrub height remained constant, whereas in natural scrub, nest height declined relative to nest shrub height. In both habitats, nests built near the top of shrubs were associated with the presence of *Smilax* spp., a perennial vine that provides dense foliage near the crown of oak shrubs. However, 68% of all nests in suburbs were associated with *Smilax*, whereas in natural scrub 9% of nest sites had *Smilax*. Few nest site characteristics, including habitat, were associated with nest failure, but nests built in oak shrubs were more successful than nests built in other vegetation. Suburban nests built near the top of relatively tall shrubs appeared to be more vulnerable to wind damage. *Received 30 July 2001, accepted 26 February 2002.*

Virtually all bird species are experiencing changes in their environment caused by humans. Measuring which anthropogenic changes might affect the survival of a species is a challenge for conservation biologists. The pace of anthropogenic changes to landscapes is so rapid that organisms may no longer be able to make optimal habitat selection decisions (Misenhelter and Rotenberry 2000, Remeš 2000), including nest site choices. Many bird species are highly selective in their choice of nest sites (Martin 1993), presumably because selection of appropriate nest sites is adaptive (Collias and Collias 1984). Certain species in the family Corvidae apparently select nest sites primarily to reduce nest predation (e.g., Hooded Crow, *Corvus corone cornix*; Loman 1979). Other corvids select sites to reduce negative effects of weather (e.g., Pinyon Jay, *Gymnorhinus cyanocephalus*; Balda and Bateman 1972). Nest site selection may result from a trade-off between opposing selective factors. For example, for some species in certain environments, the best sites to reduce predation may not be the best sites to reduce losses from inclement weather (e.g., Brown Jay, *Cyanocorax morio*; Lawton and Lawton 1980). Even within species, nest placement may vary to reflect geographic variation in climatic and biotic conditions (Schaefer 1976).

The Florida Scrub-Jay (*Aphelocoma coerulescens*) is a habitat specialist, requiring relatively open, low-growing (<2 m), oak-dominated scrub habitats. Scrub-jays typically nest in two species of oak shrubs (*Quercus geminata* and *Q. myrtifolia*), usually 1–2 m above the ground (Woolfenden 1974). Oak scrub embedded in a suburban matrix experiences reduced fire frequency, which increases the mean height of oaks and changes the oak species composition (Givens et al. 1984, Menges et al. 1993, Menges and Kohfeldt 1995). Suburban habitats also alter other ecological conditions, including the terrestrial predator community and degree of human disturbance of nesting birds (Erz 1966). Birds may nest higher in suburban habitats than in rural or natural habitats (Weber 1975, Savard and Falls 1981) because the vegetation tends to be taller, or because they are selecting sites that mitigate adverse environmental conditions endemic to suburbs. However, increasing nest height may increase the vulnerability to avian predators or susceptibility to destruction by strong winds (Graham 1988).

Here we compare nest site selection of Florida Scrub-Jays occupying natural, fire-maintained scrub to that in scrub islands embedded

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in a suburban matrix, and we examine the association of nest site characteristics with nest failure.

## STUDY AREAS AND METHODS

The two study areas were 8 km apart at the southern end of the Lake Wales Ridge in Highlands County, south central Florida (27° 15′ N, 81° 25′ W). The natural scrub area is part of the 1,968-ha Archbold Biological Station (for area description, see Abrahamson et al. 1984) and has experienced a nearly natural fire regime for at least several decades (Woolfenden and Fitzpatrick 1984). Road construction and house building began in Placid Lake Estates, the suburban study area, in the late 1950s. Since then, the natural fire regime has been altered through fire suppression and habitat fragmentation. As a result, scrub in the suburban study area is patchily distributed and overgrown.

Florida Scrub-Jays nest from late February through June. At both study areas, all jays were color marked and the populations had been studied for 24 and 2 years, respectively. During 1993 we monitored every breeding attempt of each jay family in both study areas ($n$ = 48, natural scrub; $n$ = 58, suburban scrub). We found most nests during building or egg laying. For each nest found, we recorded the plant species, height of the plant, and height of the nest to the nearest 0.1 m (from the ground to the top of the nest rim). We also recorded the presence of *Smilax* spp., a perennial vine that provides dense foliage near the crown of oak shrubs. Once found, nests were visited every 2–3 days until fledging or failure. Nests that failed were inspected for evidence of the cause of failure. Successful nests were those that fledged ≥1 young.

To measure the relative availability of shrub species and their heights, we randomly selected 10 territories in natural scrub and 14 territories in suburban scrub. At each territory, we established a transect through the longest axis of the territory. At 1-m intervals, we recorded the species and height of the nearest stem of woody vegetation >0.3 m in height (Menges et al. 1993).

During 12–15 March 1993, a severe winter storm followed by unusually cold weather struck peninsular Florida (National Oceanic and Atmospheric Administration 1993). Archbold Biological Station experienced strong west winds (13 March: >50 kph for 12 h, maximum gusts of 100 kph) and abnormally low, freezing temperatures (14–15 March: minimum daily temperatures were 3° and −2°C, respectively, approximately 9°C below the long term monthly mean). Immediately prior to the storm, 13 jay pairs were incubating on nests in the natural scrub, and 27 pairs were incubating in the suburbs. We determined the fates of these 40 nests within two days after the storm.

We tested all data for normality using a Kolmogorov-Smirnov test. Because variances around nest height were not heterogenous in either habitat, we used the nonparametric Mann-Whitney rank sum test (Mosteller and Rourke 1973) for comparisons between habitats. We used likelihood ratio chi-square tests (Siegel 1956) to compare the relative frequency of plant species used as nest sites between habitats and also patterns of use versus availability both within and between habitats. Few nests were in plants other than oaks; therefore we pooled all non-oak nest sites to ensure that <20% of the cells in the contingency table had expected values <5. We compared the height of shrubs used for nesting between habitats using an independent unpaired $t$-test (Zar 1974). Pairwise comparisons were made using the Bonferroni pairwise procedure (Miller 1985).

We analyzed data only for nests in which ≥1 egg was laid. For jay groups with more than one nest during the 1993 season, we used mean nest height and mean nest shrub height for that group. We regressed the height of the nest shrub against both absolute and relative nest heights (proportional data were arcsine transformed) and then compared the slopes of these relationships between natural scrub and the suburbs using ANCOVA. To test for selection in the height of oak shrubs used for nesting, we assigned each shrub (those available and those used as nest sites) to a height class: 1–2 m, 2–3 m, 3–4 m, >4 m. We excluded shrubs <1 m because no jay nests occurred in such low shrubs. We pooled all oaks in the analysis and excluded other shrub species used less frequently by jays for nesting ($n$ = 10 species). We used likelihood ratio chi-square tests to determine if the height distribution of all oak shrubs differed between study areas and if jays tended to select certain height classes within natural and suburban scrub. We tested for differences in the proportion of nests with *Smilax* using the Fisher exact test.

We used backwards stepwise logistic regression to determine nest site characteristics associated with nest failure. We compared all nests that fledged ≥1 young with those that failed, using habitat (natural or suburbs), shrub type (oak or not oak), nest height, the height of the nest shrub, the relative nest height (height of the nest/height of the nest shrub), and the presence of *Smilax* in the nest shrub as covariates. We performed a separate regression for nests built in oaks to determine if the species of oak chosen for nesting was associated with nest success. We compared nest height, nest shrub height, and the relative nest height of nests in the suburban area that did or did not survive the severe wind storm using ANOVA.

## RESULTS

We found 103 nests in natural scrub and 119 nests in suburban scrub. In each habitat, four species of scrub oaks accounted for >80% of nest sites (natural scrub, 88%; suburbs, 82%; Table 1). Frequency of nests placed in oaks relative to all other species did not differ significantly between the two habitats ($\chi^2$ = 1.1, df = 2, $P$ = 0.29), but frequency of the various oak species differed ($\chi^2$

TABLE 1. Plant availability versus use for nest sites of Florida Scrub-Jays nesting in two habitats during 1993, Highlands County, Florida. Values are percentages of plants in transects and plants used as nest sites.

| | Natural scrub ($n$ = 103) | | Suburban scrub ($n$ = 119) | |
|---|---|---|---|---|
| Plant species | Availability | Use | Availability | Use |
| *Quercus geminata* | 25 | 32 | 39 | 46 |
| *Q. inopina* | 19 | 30 | 20 | 30 |
| *Q. myrtifolia* | 11 | 20 | <1 | 3 |
| *Q. chapmanii* | 7 | 6 | 3 | 3 |
| *Persea humilis* | <1 | 2 | <1 | 8 |
| *Bumelia tenax* | <1 | 0 | 1 | 2 |
| *Carya floridana* | <1 | 2 | 1 | 3 |
| *Myrica cerifera* | <1 | 0 | <1 | 2 |
| *Ilex opaca* | <1 | 3 | <1 | 0 |
| *Ceratiola ericoides* | <1 | 2 | 4 | 0 |
| *Lyonia fruticosa* | 4 | 1 | 6 | 1 |
| *Ilex glabra* | 1 | 1 | 0 | 0 |
| *Rubus* spp. | 0 | 0 | <1 | 1 |
| *Serenoa repens* | 8 | 1 | 9 | 0 |
| *Ximenia americana* | <1 | 0 | 1 | 1 |
| *Asimina obvata* | 1 | 0 | <1 | 0 |
| *Lyonia ferruginea* | 1 | 0 | 3 | 0 |
| *Lyonia lucida* | 13 | 0 | 3 | 0 |
| *Pinus clausa* | <1 | 0 | <1 | 0 |
| *Pinus elliotti* | <1 | 0 | 0 | 0 |
| *Sabal etonia* | 5 | 0 | 9 | 0 |

= 18.2, df = 3, $P$ = 0.0004). In suburbs, scrub-jays used *Q. geminata* more and *Q. myrtifolia* less than did jays in natural scrub, reflecting differences in the availability of these two oak species between the two habitats. The relative use of *Q. inopina, Q. chapmanii*, and non-oak species as nest sites was similar between the two habitats.

Although we found no significant difference in the availability of oaks versus other shrubs that could be used for nesting by jays ($\chi^2$ = 0.01, df = 1, $P$ = 0.98), the distribution of individual oak species did differ between suburban and natural habitats ($\chi^2$ = 13.0, df = 4, $P < 0.001$). *Q. geminata* was more abundant and *Q. myrtifolia* less abundant in suburban scrub than in natural scrub. In each habitat, oaks were selected over other shrub species for nesting ($\chi^2$ = 9.1, df = 1, $P < 0.01$, natural scrub; $\chi^2$ = 8.2, df = 1, $P < 0.01$, suburban scrub), but individual oak species tended to be used in proportion to their availability ($\chi^2$ = 1.1, df = 1, $P > 0.50$, natural scrub; $\chi^2$ = 1.4, df = 1, $P > 0.50$, suburban scrub; Table 1).

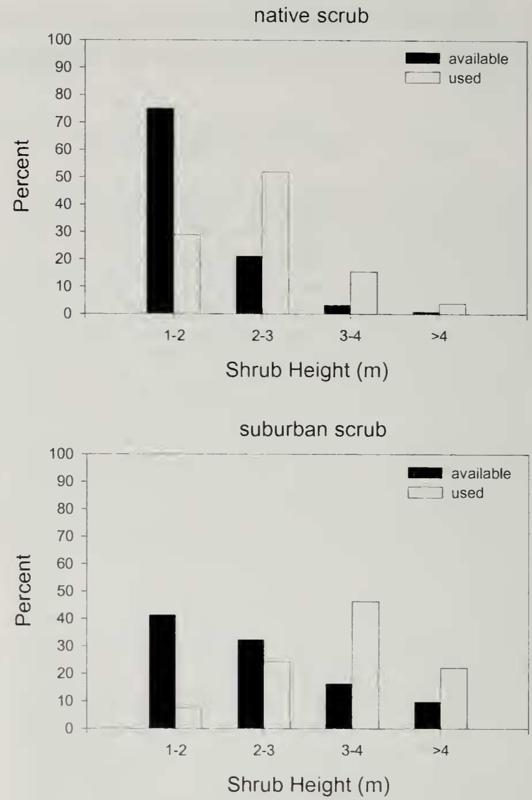


FIG. 1. Height distribution of available oak shrubs and those used by nesting Florida Scrub-Jays in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida.

Shrubs used as nest sites were significantly taller in suburban scrub than in natural scrub (mean height: 3.4 m ± 0.07 SE versus 2.4 m ± 0.11 SE; $t$ = 7.46, df = 1, $P < 0.001$) and this reflected the difference in the height of oak shrubs between the two habitats ($\chi^2$ = 138.4, df = 3, $P < 0.001$; Fig. 1). In both habitats, jays preferred to nest in shrubs slightly taller than those available ($\chi^2$ = 61.1, df = 3, $P < 0.001$, natural scrub; $\chi^2$ = 52.1, df = 3, $P < 0.001$, suburban scrub; Fig. 1). In suburbs, most (68%) shrubs used for nesting also had *Smilax* growing at or near the crown. In contrast, *Smilax* occurred in only 9% of shrubs used for nesting by jays in natural scrub. Nests also were built significantly higher above the ground in suburban than in natural scrub (2.32 m ± 0.06 SE versus 1.15 m ± 0.09 SE, respectively; $t$ = 22.5, df = 1,

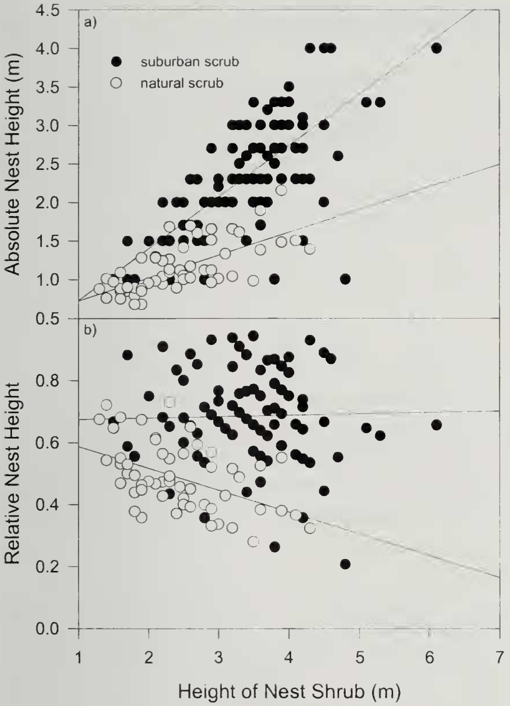


FIG. 2. Relationship between the height of the nest shrub and absolute and relative height (nest height/height of nest shrub) of Florida Scrub-Jay nests in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida. The slope of the relationships of (a) absolute and (b) relative nest height to the height of the nest shrub are significantly different (ANCOVA, $F$ = 14.8 and 7.2, $P < 0.001$ and $P = 0.008$, respectively) between the two habitats.

$P < 0.0001$). Only 2% of nests were built >2 m above ground in natural scrub ($n$ = 103) compared to 76% in suburban scrub ($n$ = 119). Relative nest height also was greater in suburban scrub than in natural scrub (mean 62.0% ± 0.01 SE, natural scrub; 76.8% ± 0.01 SE, suburban scrub; $t$ = 7.4, df = 1, $P < 0.001$).

Nest height increased with the height of the nest shrub in both habitats, but more so in suburbs (Fig. 2a). In suburbs, relative nest height was constant regardless of the height of the nest shrub. In natural scrub, the relative nest height declined as the height of the nest shrub increased (Fig. 2b). Nests rarely were built in the lower third of a shrub in either habitat. However, because *Smilax* proliferates at the top of shrubs, the relative height of nests built in shrubs with *Smilax* was higher than those built in shrubs without this perennial vine in both habitats (Fig. 3).

Using logistic regression, we could not discriminate between successful and unsuccessful nests based on habitat, nest height, height of the nest shrub, relative nest height, and presence of *Smilax*; however, nests built in oaks tended to be more successful than those built in other vegetation (B = 5.01, Wald statistic = 4.12, df = 1, $P = 0.043$). For nests built in oaks, none of the above variables nor oak species was significantly associated with nest success. Although nest success did not differ significantly between natural scrub and suburbs (40.4% versus 47.8%, respectively), causes of nest failure differed ($\chi^2 = 6.67$, df = 2, $P = 0.036$) between the two habitats. While predation rates (0.65 versus 0.71) and abandonment rates (0.16 versus 0.25) were statistically similar between suburbs and natural scrub, weather-related losses were significantly higher in suburbs (0.19 versus 0.04).

Most weather-related losses in 1993 in suburbs occurred during the March storm, largely because of wind. Some nests literally were blown out of the nest shrub. Eggs, either broken or intact, were found below several nest sites. In suburbs, 11 of 27 nests active at the time of the storm failed. These failures included two nests that were deserted, probably because of heavy rains and cold temperatures as well as strong winds. Thus, conservatively, 33.3% of active nests (nine of 27) failed because of strong winds. In natural scrub, only two of 13 nests active during the storm failed, and of these only one could be attributed to wind. Thus, in natural scrub only 7.7% of active nests (one of 13) failed because of wind. These differences are marginally significant ($\chi^2 = 3.56$, df = 2, $P = 0.059$). Within the suburbs, nests that failed because of wind were built significantly closer ($F_{1,26} = 6.1$, $P < 0.05$) to the top of relatively tall shrubs (Table 2) and were more likely to be built in shrubs with *Smilax* ($\chi^2 = 6.4$, df = 1, $P = 0.018$) than those that survived the storm (63.6% versus 16.7%, respectively). Only nests built >2.0 m above the ground experienced wind damage.

## DISCUSSION

Change in vegetation structure is known to influence intraspecific nest site selection at

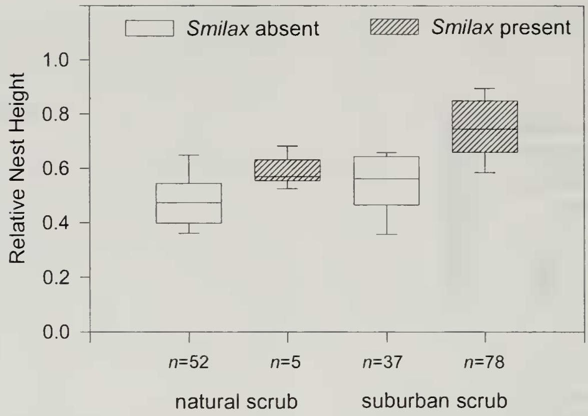


FIG. 3. Relationship between the presence or absence of *Smilax* and the relative height (nest height/height of nest shrub) of Florida Scrub-Jay nests in native, undisturbed scrub and in a suburban matrix of disturbed scrub during 1993, Highlands County, Florida. The box indicates the 25th and 75th percentile of relative nest heights, the solid bar within the box indicates the 50th percentile. The capped bars indicate the 10th and 90th percentiles.

broad geographic scales (Schaefer 1976), regional scales (Bekoff et al. 1987, Graham 1988) and local scales (Root 1967, Van Riper 1976). Suburbanization has many impacts on vegetation structure and composition (DeGraaf 1985), yet oak shrubs apparently suitable for Florida Scrub-Jay nesting remained abundant in our suburban area. As a result, scrub-jays used remarkably similar nest sites in the two habitats even though the relative availability of various shrub species of different heights differed. In both habitats, most nests were constructed in scrub oaks and nest height was proportional to the height of the shrub in which the nest was built. In the suburbs, jays used the four different oak species for nesting in different proportions than in natural scrub and their nests tended to be built higher above the ground. Both these differences are consistent with the structure and composition of available oak shrubs in suburbs, likely the result of fire exclusion. Oak species composition in scrub habitat changes in the absence of fire, with *Q. geminata* tending to increase in abundance with time since fire (Menges et al. 1993, Menges and Kohfeldt 1995). Because jays appear to select *Q. geminata* disproportionately for nesting in both suburbs and natural scrub (Woolfenden 1974), their increased use of this plant in fire-suppressed habitat was not surprising.

Most scrub oaks have numerous, stiff, divergent twigs which provide a solid nest foundation, protection, and concealment for the incubating jay. Relatively few other plant species common in natural scrub provide such nest sites. Therefore, in natural scrub, Florida Scrub-Jays rarely nest in vegetation other than oaks. The most frequent examples are rosemary (*Ceratiola ericoides*), crookedwood (*Lyonia ferrugenia*), fetterbush (*L. lucida*), scrub holly (*Ilex opaca*), young pines (*Pinus* spp.), and saw palmetto (*Serenoa repens*; Woolfenden 1974), which together constitute

TABLE 2. Proportion of Florida Scrub-Jay nests that survived a severe wind storm on 13 March 1993 in two different habitats, Highlands County, Florida. Values for nest height and relative nest height are means ± 1 SE.

| | Proportion of nests | | Nest height (m) | | Relative nest height[a] | |
|---|---|---|---|---|---|---|
| Habitat | failed | survived | failed | survived | failed | survived |
| Natural scrub (*n* = 13) | 0.08 | 0.92 | 1.2 ± 0.1 | 1.1 ± 0.2 | 0.47 | 0.49 ± 0.1 |
| Suburban scrub (*n* = 27) | 0.33 | 0.67 | 2.6 ± 0.5 | 1.8 ± 0.6 | 0.72 ± 0.1 | 0.59 ± 0.2 |

[a] Nest height/height of the nest shrub.

the densest shrubs in the Florida scrub other than oaks.

In suburban habitats, native birds may nest in exotic vegetation structurally similar to native vegetation, especially when native vegetation is rare or absent (Emlen 1974, Mills et al. 1989). In southwest Florida, where scrub-jays inhabit suburbs much older than our suburban study site, little (if any) native scrub vegetation remains and scrub-jays regularly nest in exotic shrubs (J. Thaxton pers. comm.). However, in our suburban study area where several species of exotic shrubs with growth characteristics similar to the oaks (e.g., *Viburnum*, *Ligustrum*, *Podocarpus*, *Citrus*) were common, jays almost always nested in the native species, especially oaks. Selection of oaks for nesting may be adaptive because nests built in oaks are more likely to succeed.

Suburban scrub-jays built their nest higher relative to the height of the nest shrub. The foliage of *Smilax* vines lies atop many shrubs, where it provides dense cover for bird nests. *Smilax* appears to be more abundant in suburban habitat, perhaps because of fire suppression or physical disturbance (Menges and Kohfeldt 1995). In both habitats, nests built near the tops of the nest shrubs were associated with *Smilax*. Suburban scrub-jays probably build their nests higher relative to the height of the shrub because *Smilax* is more common in this habitat.

Height alone may not be the most important criterion in nest site selection in suburban habitats (Graham 1988, but see Preston and Norris 1947, Weber 1975). In natural scrub, oak shrubs have relatively dense foliage from the crown to the base and jay nests are well concealed. With fire suppression, oak shrubs become trees and foliage tends to be denser near the crown and thinner toward the base. If jays seek to conceal their nests, they may build it near the densest foliage. Although we did not measure foliage density or nest concealment, nests associated with *Smilax* appear to be well concealed. Alternatively, suburban birds may nest higher in shrubs to avoid predators more common in suburbs (e.g., domestic cats, humans). However, in an urban population of American Robins (*Turdus migratorius*), habitat structure, measured largely by foliage volume, was the main determinant of nest height (Savard and Falls 1981).

Predation is the major cause of nest failure in scrub-jays (Woolfenden and Fitzpatrick 1984, Schaub et al. 1992) and jays probably select sites to minimize the probability of detection by these predators. Suburban scrub-jays likely perceive *Smilax*-crowned oak shrubs as suitable nest sites. Because none of the nest site characteristics, other than the use of oaks for nesting, could be associated with nest success, it appears that the stereotypical nest sites selected in both habitats were equally effective at deterring predation. Oak shrubs appear to provide the best nest sites for Florida Scrub-Jays, regardless of whether they occur in natural fire-maintained scrub or in fire-suppressed suburban scrub.

Perhaps surprisingly, habitat itself was not associated with nest success. In a separate analysis, we found no differences in success (defined as the probability of fledging $\geq 1$ young) between jay nests in our suburban and natural scrub study areas over 8 years (Bowman and Woolfenden 2001). However, differences in the timing of nesting failure between the two habitats suggest that the two predator communities differ. Indeed, predator communities commonly differ between suburban and natural habitats (Tomialojc 1970, Churcher and Lawton 1987; A. L. Fleischer and RB unpubl. data), even though nest success of some suburban birds often is equal to that of birds in more natural settings (Gutherie 1974, Gering and Blair 1999, Bowman and Woolfenden 2001, but see Emlen 1974, Beissinger and Osborne 1982, Tweit and Tweit 1986, Mills et al. 1989). These patterns suggest that suburban birds may select nest sites that are appropriate to the local predator community.

Causes of nest failure other than predation are rare in scrub-jays. Wind accounts for very few failures ($<1\%$ over 10 years; Woolfenden and Fitzpatrick 1984), so nest site selection probably has little to do with ameliorating the effects of wind. In natural scrub, nests well concealed from predators also are likely sheltered and stable, and thus likely little affected by strong wind. In suburbs, nest sites that afford effective concealment from predators may be less sheltered and stable, located near the tops of relatively tall shrubs, and thus, may be more vulnerable to wind, as seen in our study area in 1993. In suburbs, predation and weather may be opposing potential selective factors. Storms of the magnitude of the one causing wind-related nest failure in this study are relatively rare and may not be a sufficient selective pressure to offset predation as the driving force for nest site selection. However, as habitats are rapidly altered by humans, behaviors such as nest site selection, that have evolved and are successful in native habitats, may become increasingly maladaptive in anthropogenic landscapes (Misenhelter and Rotenberry 2000, Remeš 2000).

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